Estuarine, Coastal and Shelf Science 215 (2018) 241–249

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Mangrove mortality in a changing climate: An overview

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A B S T R A C T

Mangroves provide vital ecosystem services at the dynamic interface between land and oceans. Recent reports of mangrove mortality suggest that mangroves may be adversely affected by climate change. Here, we review historical mortality events from natural causes (all mortality other than deforestation, land use change and pollution) and provide a global assessment of mortality drivers. Since the 1960's approximately 36,000 ha of mangrove mortality has been reported (0.2% of total mangrove cover in 2011) in 47 peer reviewed articles. Due to the uneven global distribution of research effort, it is likely that mangrove mortality events go unreported in many countries. It is therefore difficult to assess temporal changes in mortality due to the small number of reports and increasing effort in observations in recent years. From the published literature, approximately 70% of reported mangrove loss from natural causes has occurred as a result of low frequency, high intensity weather events, such as tropical cyclones and climatic extremes. Globally, tropical cyclones have caused the greatest area of mangrove mortality, equivalent to 45% of the reported global mangrove mortality area from events over six decades. However, recent large-scale mortality events associated with climatic extremes in Australia account for 22% of all reported historical forest loss. These recent mortality events suggest the increasing importance of extreme climatic events, and highlight that mangroves may be important sentinels of global climate change. Increasing frequency, intensity and destructiveness of cyclones as well as climatic extremes, including low and high sea level events and heat waves, have the potential to directly influence mangrove mortality and recovery, particularly in mid latitudes.

1. Introduction

Mangrove forests provide a wide range of highly valuable ecosystem services, including support of biodiversity and fisheries, coastal protection, carbon sequestration and nutrient processing (Barbier et al., 2011). These forests sequester large amounts of carbon from the atmosphere into their biomass and soils (Mcleod et al., 2011), and contribute to marine food webs via the detrital energy flow pathways (Lugo and Snedaker, 1974; Dittmar et al., 2006, Abrantes et al., 2015). The collective economic valuation of mangrove ecosystem services has been estimated to be worth USD 194,000 per hectare per year, with a global value of USD 2.7 trillion per year (Barbier et al., 2011; Costanza et al., 2014).

Despite their importance, extensive deforestation of mangroves has occurred (Hamilton and Casey, 2016; Richards and Friess, 2016). Further, anthropogenic activities such as changes in hydrology, add synergistic stressors to mangrove forests, reducing ecosystem function and ecosystem service value (Lewis et al., 2016). Although deforestation has been the major cause of forest loss in the past, mangrove loss from various natural and anthropogenic disturbances have also been reported in the literature (Jimenez et al., 1985). Mangroves are also susceptible to climate change, which has been anticipated to have widespread negative consequences for mangrove distribution (Lovelock et al., 2007; Alongi, 2008; Gilman et al., 2008). However, few studies have unequivocally demonstrated the effects of climate change on mangroves.

Recent reports of mangrove mortality in Australia (Duke et al., 2017a; Lovelock et al., 2017) and elsewhere (Albert et al., 2016; Servino et al., 2018) suggest that the incidences of mangrove mortality may be increasing due to climate change. However, most research on the effects of climate change on mangroves has focused on temperature driven effects such as poleward expansion and sea level rise (Gilman et al., 2008; Lovelock et al., 2015; Kelleway et al., 2017; Osland et al., 2017a). A global analysis of mangrove mortality has not been performed since Jimenez et al. (1985) collated reports of mangrove mortality three decades ago. Here we review global records of mangrove losses from natural events, and analyse the environmental factors causing these losses. We consider the impacts of climate change to mangroves to be a natural phenomenon since we cannot distinguish individual climatic events as natural or anthropogenic. However, it is

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https://doi.org/10.1016/j.ecss.2018.10.011
Received 3 May 2018; Received in revised form 10 October 2018; Accepted 15 October 2018
Available online 17 October 2018
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Table 1
Definitions of terms.

Term	Definition
Dieback	Canopy loss that may or may not lead to forest mortality.
Mortality	Forest death caused by disturbance and/or change in environmental conditions.
Climatic extremes	Climatic events such as drought, flood, extreme heat or cold, extreme sea level variation, localized weather events and intense wind or wave energy. Defined by Smith (2011) as the "occurrence in which a statistically rare or unusual climatic period which has potential to alter ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability". The response of mangroves to these climatic extremes is site and species specific.
Extreme climatic event	An extreme ecosystem response to climatic extremes, beyond the ecosystems normal range of variability (Smith, 2011).
Sea level variability	Short term (days to months) increase or decrease in regional sea level caused by atmospheric pressure, winds, air/sea temperature, freshwater inputs and ocean currents.
Sea level rise	Long-term global increase in sea level.

clear that anthropogenic activities which induce change to the global climate will influence individual climatic events and the future mangrove distribution (Harris et al., 2017; Lovelock et al., 2007; Alongi, 2008, Gilman et al., 2008).

2. Historical mortality reports and emerging trends

Here we differentiate between mangrove forests which have undergone disturbance yet have the ability to recover (dieback) and the death of a forest related to a disturbance (mortality) which does not have the ability to recover in the existing environmental conditions (Table 1). We also differentiate between tree mortality (individual level) and forest mortality (ecosystem level). Forest and individual tree recovery can include processes such as re-sprouting (coppicing) or regeneration via propagule recruitment. The time frame of this recovery may range from years to decades, depending upon the nature of the mortality event and the resilience of the forest. Inability to recover can be caused by permanent changes in environmental conditions that prevent recovery (e.g. subsidence, erosion or permanent changes in hydrology). Mangrove mortality from natural causes is reported for every continent where mangroves are found, however the highest frequency of mangrove mortality is reported from the Caribbean and the Gulf of Mexico (Fig. 1; Table 2). To our knowledge, excluding deforestation, forest mortality areas exceeding 5000 ha have only been reported from Australia (Duke et al. (2017a)). Considering the uneven global distribution of research effort, it is likely that mangrove mortality events may go unreported in many countries.

Over short time scales, mangrove forests experience daily tide fluctuations, which can significantly influence water availability, soil salinity and anoxia, with a direct effect upon plant growth and fitness (Ball, 1988). Over longer time scales, mangroves have experienced large displacements in their distribution due to historical sea level change over the Holocene (Woodroffe and Grindrod, 1991) and over shorter time scales (years, decades) due to varying sediment supply (Woodroffe et al., 2016). Mangroves can undergo rapid contraction in cover when conditions are suboptimal (Eslami-Andergoli et al., 2015) or expansion under favourable conditions (Asbridge et al., 2016). On a global scale, mangrove mortality due to natural causes has been reported over scales ranging from 1 to 7400 hectares (Fig. 1; Table 2) with a total area of forest mortality reported since the 1960s of approximately 36,000 ha (0.2% of total mangrove cover in 2011).

Assessment of mangrove mortality over time (decadal increments) indicates a general increase in mortality area each decade since the 1940's (Fig. 2). Climatic extremes and tropical cyclones account for ~80% of the mangrove mortality area reported since 1990. The increasing mangrove mortality area observed each decade may be due to increasing research effort and advances in remote sensing technology, thus the trend of increasing mortality area observed here may not necessarily be related to increasing mangrove mortality, but may represent a research effort bias. When the area of mortality is adjusted for research effort (standardized using the number of publications returned using a search on "mangrove" in the Web of Science for each decade), no significant trend is observed (not shown).

The global distribution, abundance and species richness of mangrove forests is controlled by climatic parameters, predominantly rainfall and temperature (Osland et al., 2017b). However, these climatic parameters are strongly influenced by regional scale processes. Therefore, forest distributions are often largely controlled by regional and local scale environmental controls such as temperature, precipitation, tidal amplitude, wave energy and riverine inputs (Alongi, 2008). Natural events that cause mangrove mortality can result from individual and/or synergistic changes in environmental conditions that

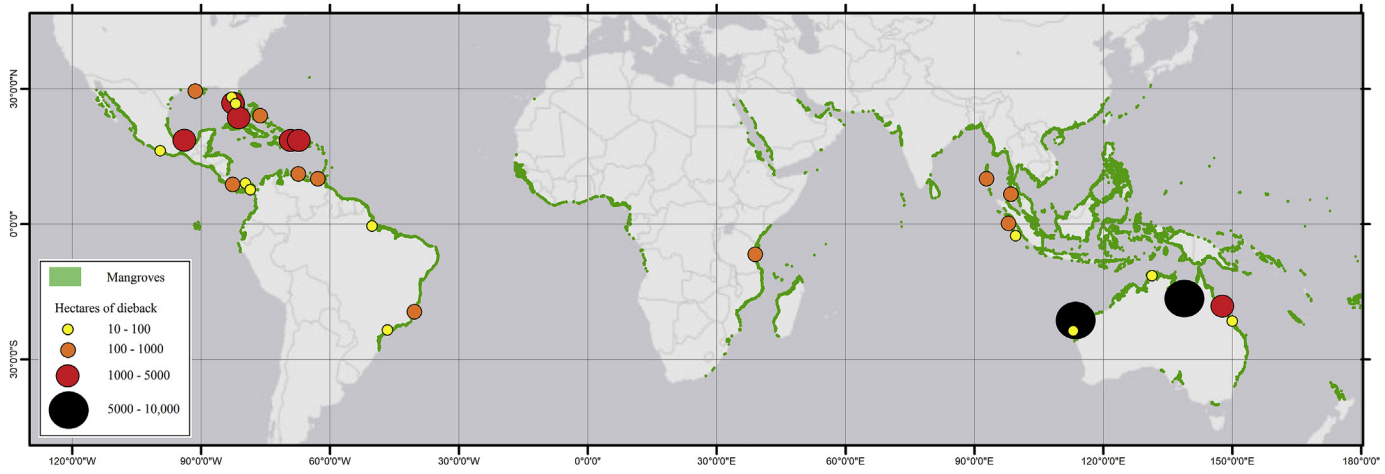

Fig. 1. Global mangrove area along with the location and extent of mangrove mortality events driven by natural causes. Image of global mangrove area is modified from (Giri et al., 2011).

Table 2
Summary of reported mangrove mortality from natural causes reported in peer reviewed literature expanded from Jimenez et al. (1985). For review of mortality events in plantations and restored forests see López-Portillo et al. (2017).

Site	Date	Cause	Area (ha)	Source
Tropical cyclones				
Florida, USA	1935	Labor Day Hurricane	Extensive	(Wanless and Vlaswinkel, 2005; Smith et al., 2009)
Puerto Rico	1956	Hurricane Betsy	< 5*	(Wadsworth and Englerth, 1959)
Florida, USA	1960	Hurricane Donna	~4000**	(Craighead and Gilbert, 1962)
Florida, USA	1960	Hurricane Donna	Patches	(Craighead, 1964)
Belize	1961	Hurricane Hattie	Patches	(Vermeer, 1963)
Australia	1971	Cyclone Althea/siltation	~5*	(Heinsohn and Spain, 1974)
Nicaragua	1988	Hurricane Joan	~5*	(Roth, 1992)
Florida, USA	1992	Hurricane Andrew	150	(Ogden, 1992)
Dominican Republic	1998	Hurricane Georges	2240	(Sherman et al., 2001)
Honduras	1998	Hurricane Mitch	490*	(Cahoon et al., 2003)
Australia	1999	Cyclone Vance	5700	(Paling et al., 2008)
Micronesia	2004	Cyclone (Typhoon) Sudal	< 10*	(Kauffman and Cole, 2010)
Florida, USA	2005	Hurricane Wilma	1250	(Smith et al., 2009)
Philippines	2009	Typhoon Chan-hom	Extensive	(Salmo et al., 2014)
Australia	2011	Cyclone Yasi	2200	Asbridge et al., (in review)
Climatic extremes				
Puerto Rico	1937–1972	Hypersalinity	Fringes	(Cintrón et al., 1978)
South Africa	1965	Flooding	~10	(Breen and Hill, 1969)
Florida, USA	1983	Freeze	~1	(Montague and Odum, 1997)
Gulf of Mexico, USA	1930–1980	Freeze	Extensive	(Sherrod and McMillan, 1981)
Gulf of Mexico, USA	1983	Freeze	Extensive	(Sherrod and McMillan, 1985)
Guadeloupe	–	Hypersalinity	Extensive	(Servant et al., 1978) as cited in Jimenez et al. (1985)
Java	–	Flooding/siltation	42	(Soerianegara, 1968) as cited in Jimenez et al. (1985)
Florida, USA	–	Frost	Extensive	(Lugo and Patterson-Zucca, 1977) as cited in Jimenez et al. (1985)
Texas	–	Frost	Patches	(West, 1977) as cited in Jimenez et al. (1985)
Gulf of Mexico, USA	1983 and 1989	Freeze	Extensive	(Lonard and Judd, 1991)
Florida, USA	1980's	Freeze	15	(Stevens et al., 2006)
Senegal	1990's	Drought	Extensive	(Diop et al., 1997)
Australia	1994	Hail storm	0.1	(Houston, 1999)
Venezuela	1990–1998	ENSO related drought	880	(Barreto et al., 2008; Otero et al., 2017)
Tanzania	1997	Flooding	117	(Erftemeijer and Hamerlynck, 2005)
Kakadu, Australia	2015–2016	ENSO related climatic extremes	Extensive	(Lucas et al., 2018)
Mangrove Bay, Australia	2002–2003, 2015–2016	ENSO related climatic extremes	40	(Lovelock et al., 2017)
Gulf of Carpentaria, Australia	2015–2016	ENSO related climatic extremes	~7400	(Duke et al., 2017a)
Brazil	2016	Hail storm	~500	(Servino et al., 2018)
Tsunamis				
Dominican Republic	1946	Dominican Republic Tsunami	~4500	(Sachtler, 1973) as cited in Jimenez et al. (1985)
Indonesia	2004	Banda Aceh, Tsunami	300–750	(BAPPENAS, 2005)
Thailand	2004	Banda Aceh, Tsunami	1050	(Kamthonkiat et al., 2011)
Great Nicobar Island, India	2004	Banda Aceh, Tsunami	530	(Sridhar, 2007)
Thailand	2004	Banda Aceh, Tsunami	patches	(Fujioka et al., 2008)
Thailand	2004	Banda Aceh, Tsunami	~1*	(Yanagisawa et al., 2010)
Andaman Islands	2004	Banda Aceh, Tsunami	Patches	(Roy, 2016)
Herbivores and pathogens				
Australia	1980	Pathogen	Patches	(Weste et al., 1982)
Malaysia	1990's	Herbivory	Patches	(Jin-Eong, 1995)
India	2000	Herbivory	Patches	(Kathiresan, 2003)
Kenya	2005	Herbivory	Patches	(Jenoh et al., 2016)
Mexico	2010	Herbivory	3846	(Sánchez et al., 2018)
Other				
Bahamas	2011	Cumulative stressors	120	(Rossi, 2018)
The Gambia	1970's	Uncertain	2211	(Blasco, 1983)
Bermuda	1800's - 1993	Sea level rise	1	(Ellison, 1993)

*Mortality areas are estimated from descriptions of the mortality and the mangrove area at the sites.

exceed mangrove physiological limits (Table 3).

2.1. Tropical cyclones

Extreme storms have caused the greatest global area of mangrove mortality, equivalent to 45% of the reported global mangrove mortality area (Table 2; Fig. 2). In the last five decades the percentage of mangrove mortality caused by tropical cyclones has remained relatively constant, accounting for 30–60% of the total mortality area (Fig. 3). Tropical cyclones generate strong winds, flooding rain, high-energy waves and storm surges that can negatively affect coastal wetlands (Table 3). Individual events have caused damage to areas up to 28,000 ha (Villamayor et al., 2016) and forest mortality in areas of up to 5700 ha (Table 2).

Storm trajectories have high inter-annual variability, yet broad cyclone paths exist due to oceanic boundary conditions and sea surface temperatures (Ulbrich et al., 2009). For example, the Gulf of Mexico is frequently affected by hurricanes which have caused considerable mangrove damage and mortality (Table 2, Craighead, 1964, Smith et al., 2009). Indeed, coastal ecosystems along the Gulf of Mexico have been subject to one major hurricane every 3 years over the last century (Diaz and Pulwarty, 2012). Cumulative impacts from reoccurring

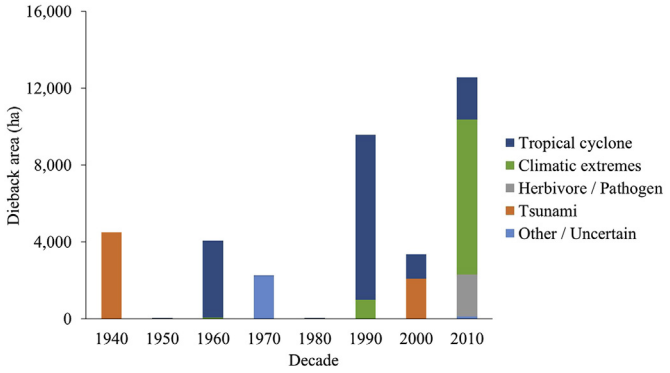

Fig. 2. Summary of decadal trends of total global area of mangrove mortality from various natural causes reported in peer reviewed literature summarized in Table 2.

mortality events related to hurricane frequency are not well understood, but can clearly influence recovery and may be related to permanent ecosystem changes in some cases (Smith et al., 2009; Feller et al., 2015).

The northern hemisphere experiences ~70% of global cyclones/hurricanes (Knutson et al., 2010a) and 76% of reported cyclone mortality events (Table 2), yet these reports only account for 51% of the global cyclone related mortality area (Table 2). Nearly 100% of cyclone associated mangrove mortality reported in the Southern hemisphere has occurred in Australia, perhaps due to larger research effort. The relative importance of cyclone associated mortality has declined in the last decade as mortality associated with climatic extremes has increased (Fig. 3).

2.2. Climatic extremes

In previous centuries, mangrove coverage at high latitudes has been controlled by extreme cold events causing frost/freezes (Sherrod and McMillan, 1981, Sherrod and McMillan, 1985; Osland et al., 2017a). This is still the case in many continents, however poleward expansion of mangroves, and encroachment into saltmarsh is already occurring as global temperatures increase (Saintilan et al., 2014). Prior to the 1980's, mangrove forest mortality had not been attributed to climatic extremes other than frost/freeze events (Table 2). In the past decade, extreme climatic events have accounted for 22% of the reported global forest loss (Fig. 3) and 98% of this mortality have been due to drought and regional sea level variability. El Niño Southern Oscillation (ENSO) are large scale weather patterns influencing seasonal rainfall and sea levels (Moon et al., 2015; Widlansky et al., 2015). ENSO driven low sea level and high temperatures have severe impacts on nearshore ecosystems and the reoccurrence intervals of these events may be critical for slow recovering coastal ecosystems such as mangroves (Glynn, 1988). Strong ENSO events will clearly play an important role in mangrove mortality events into the future.

In Australia and the Eastern Pacific, mangrove mortality associated with drought is overwhelmingly associated with ENSO events. A recent mortality event in the Gulf of Carpentaria (northern Australia) is unprecedented in areal extent and was attributed to the combined climatic extremes associated with a severe El Niño event (Duke et al., 2017a; Harris et al., 2017). Other recent mangrove forest mortalities due to extremes in temperature, drought, localised weather events and regional sea level variability have occurred in Exmouth in Western Australia, Kakadu in North Western Australia, the Sundarbans and Brazil (Paul et al., 2017; Lovelock et al., 2017; Lucas et al., 2018; Servino et al., 2018).

Prior to these recent events, few studies had observed extensive drought related mortality (Fig. 2). El Niño associated drought caused 880 ha of mangrove forest mortality in Venezuela during a period from 1990 to 1994 and during an intense El Niño period from 1997 to 1998 (Table 2, Barreto et al., 2008; Otero et al., 2017). In these cases, mangrove forests showed no recovery nine years later, due to peat oxidation and sediment subsidence that fundamentally changed the suitability of the site for mangrove growth (Otero et al., 2017). El Niño associated drought also caused substantial stress to mangrove forests in Micronesia, with reports of a two fold increase in porewater salinity, although no tree mortality was reported (Drexler and Ewel, 2001). Severe drought in the Eastern Pacific associated with La Niña has also caused a massive mortality of salt marsh in 2000, affecting an area of 100,000 ha equivalent to 41% of contiguous coastal wetlands in the United States (McKee et al., 2004).

2.3. Tsunamis

The frequency of large tsunamis is approximately 10% that of extreme storm events (Marois and Mitsch, 2015; Webster et al., 2005). However, tsunamis have accounted for 18% of historical mangrove mortality and have historically accounted for some of the largest recorded mangrove mortality events (Fig. 2). The 2004 Indian Ocean earthquake triggered a series of devastating tsunamis that resulted in the loss of 1880–2330 ha of mangroves, as well as massive damage to coral reefs, sand dunes, forests, groundwater reserves, and to human settlements and agricultural lands (Kamthonkiat et al., 2011). GIS analysis of forests damaged by the 2004 tsunami revealed that approximately half of affected forest areas experienced total destruction, while half experienced severe damage that removed most trees (Kamthonkiat et al., 2011).

The first report of a major mangrove mortality caused by a tsunami was in 1946 in the Dominican Republic, which caused a mortality area

Table 3
Causes of mangrove mortality or dieback from natural events.

Disturbance	Cause of forest mortality or dieback	References
Tropical cyclones	Strong winds, flooding rain, high-energy waves and storm surges. Effects include physical damage to canopies and soils (erosion); and sedimentation and flooding which limit oxygen supply to roots.	(Paling et al., 2008, Smith et al., 2009, Kauffman and Cole, 2010)
Heat waves/frost	At temperatures exceeding 38–40 °C, photorespiration increases while photosynthesis is inhibited. Evaporation increases with high temperatures which increases water loss and risk of desiccation. Frost/freezes result in tissue damage and hydraulic failure at high latitudes.	(West, 1977, Rennenberg et al., 2006, Stuart et al., 2007, Lindner et al., 2010)
Drought	Drought stress is directly related to the development of hypersaline soil conditions. Low rainfall and groundwater inputs reduce water availability and high temperatures increase evaporation and evapotranspiration resulting in hydraulic failure and desiccation.	(Hoppe-Speer et al., 2013, Ward et al., 2016)
Tsunamis	Extreme physical damage to canopies and soils (erosion). Sedimentation and flooding which limit oxygen supply to roots.	(Kamthonkiat et al., 2011; Sachtler, 1973
Herbivores and pathogens	Pathogens - leaf damage and wood decomposition in living plants, including symptoms such as butt, heart and root rot. Herbivores – tree defoliation and loss of photosynthetic function.	(Hyde et al., 1998). (Osorio et al., 2016)

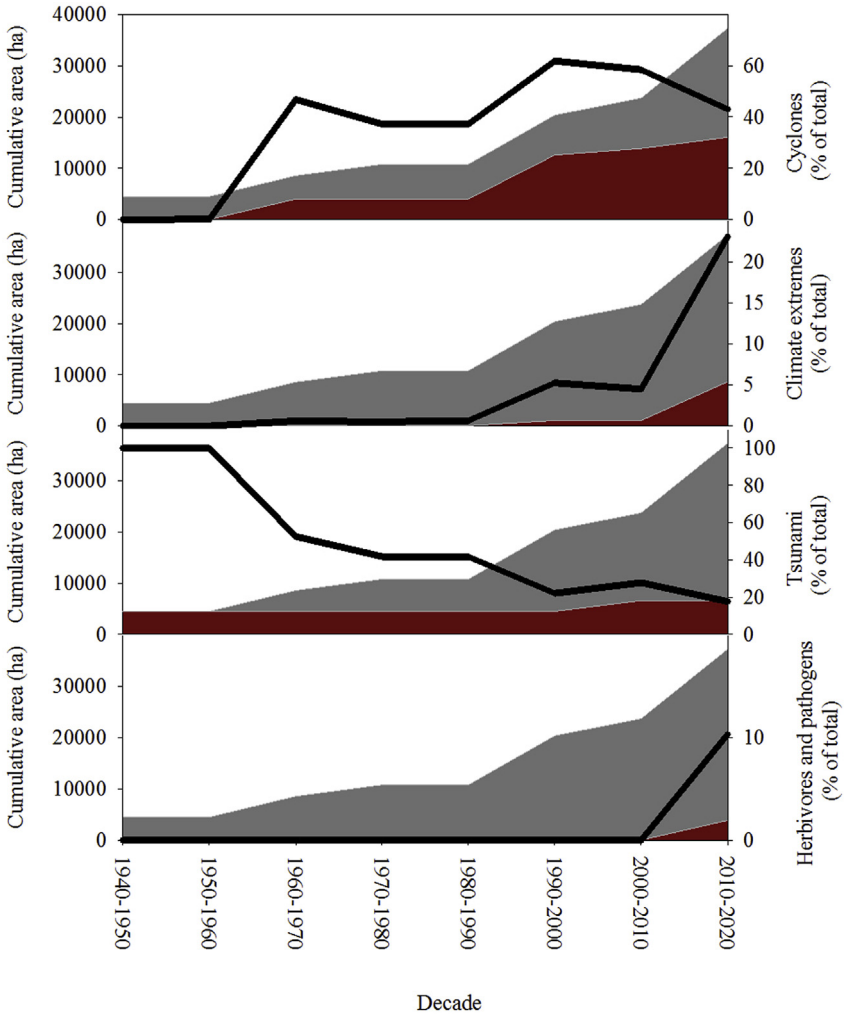

Fig. 3. Total cumulative mortality area (grey), cumulative areas (red) of a) cyclones, b) climate extremes, c) tsunamis and d) herbivores and pathogens. The percentage of mortality from each individual cause of the total mortality area per decade (black line). Mortality area from 49 peer reviewed reports. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

estimated at 4500 ha (Sachtler, 1973, Jimenez et al., 1985). Since this event, only one other significant forest loss associated with tsunami has been reported (Indian Ocean, 2004 tsunami). Because tsunami related dieback is uncommon and sporadic, the apparent decrease in total mangrove mortality area over time caused by tsunamis should be interpreted with care, since other natural causes have caused increasingly extensive areas of forest mortality (Fig. 3).

2.4. Herbivores and pathogens

Historically, while several works document insect infestations in mangroves (e.g. Feller and Mathis, 1997; Feller and McKee, 1999; Reef et al., 2012), few cases have reported significant forest loss from herbivores and pathogens. Cases of tree mortalities caused by wood borer insects (Feller, 2002), defoliation (Anderson and Lee, 1995; Jin-Eong, 1995, Mehlig and Menezes, 2005) and pathogens (Pegg et al., 1980) have been reported, but only in small, isolated patches. Jenoh et al. (2016) describe serious damage to extensive areas of mangrove forests in Kenya from two species of wood boring insects, which caused patches of forest dieback. These smaller scale losses of forest area or canopy may cause a reduction in ecosystem services by changing forest structure and function (Jennerjahn et al., 2017), which can also decrease forest resilience.

Recently, Sánchez et al. (2018) report the first case of extensive forest mortality from herbivory in Mexico 2010 (Table 2: Fig. 3). In this case a mangrove forest area of 3846 ha was severely damaged from defoliation caused by an overpopulation of the caterpillar *Anacamptodes sp,* resulting in an area of 2196 ha of forest mortality (Sánchez et al., 2015, 2018). Herbivores and pathogens may stress forests and cause forest mortality in combination with other stressors (Rossi, 2018).

3. Future outlook

3.1. Tropical cyclones

Cyclone intensity, destructiveness and frequency has increased since the 1970's (Hartmann et al., 2013). While this trend may have large regional differences (Knutson et al., 2010a; Wong et al., 2014), cyclone intensity is predicted to continue to increase in areas where mangrove mortality is already occurring (Fig. 4). These climatic projections compared with historic mortality events suggest an increasing threat to non-equatorial mangroves, which may be increased in areas affected by human activities, for example nutrient enrichment (Feller et al., 2015). Intensified temporal clustering of cyclones is considered a major contributor to coral reef decline (Wolff et al., 2016) and could have similar impacts on mangrove ecosystems through reduction in recovery time, although they may also enhance dispersal of mangrove propagules (Dangremond and Feller, 2016) and delivery of nutrients and freshwater (Adame and Lovelock, 2011). Modelling suggests that cyclones will have enhanced precipitation and increased latitudinal range into

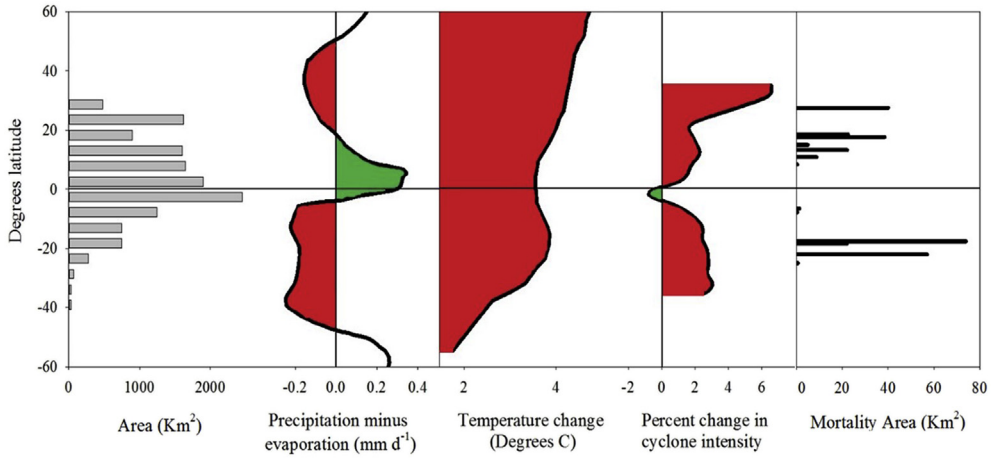

Fig. 4. Projected or measured influence of global climate change on climatic variables. a) Mangrove area (Giri et al., 2011), b) mean predicted precipitation minus evaporation (mm d^{-1}) over land and ocean (Byrne and O'Gorman, 2015), c) predicted temperature change (°C) for 2080–2099 (Meehl et al., 2007), d) modelled poleward shift in cyclone activity measured between 1980 and 1994 to 1995–2010 (Kossin et al., 2014) and e) The area and latitude of individual mangrove mortality events associated with climatic disturbance as reported in peer reviewed literature (See Table 2).

the future due to climate change, but there are high levels of uncertainty in these models (Wong et al., 2014; Scoccimarro et al., 2017).

3.2. Climatic extremes

The increasing trend in mangrove mortality due to climate extremes (Fig. 3) may be associated with climate change and could increase as climate change progresses. However this may be counterbalanced to some extent by increasing poleward expansion (Cavanaugh et al., 2014; Osland et al., 2017a). For example, extensive losses of mangrove coverage have occurred historically due to periods of subfreezing temperature (Sherrod and McMillan, 1981, Sherrod and McMillan, 1985). Reduction in frequency of freezing events is already allowing for range expansion of mangroves to higher latitudes (Osland et al., 2017a). In addition, increasing precipitation in low latitudes may benefit equatorial mangrove forests (Sanders et al., 2016). However, increased precipitation may also lead to increased siltation/sedimentation, which could have adverse effects (Ellison, 1999). Projected changes to precipitation, evaporation and temperature will also result in reduced water availability to non-equatorial mangroves (Fig. 4).

Increased mortality due to aridity driven by climate change was predicted for Central America, the Caribbean and North Western Australia (Record et al., 2013; Alongi, 2015). The intensity of El Niño events in the Pacific Ocean has increased by approximately 50% in the last 30 years (Lee and McPhaden, 2010; Cai et al., 2014). This is increasing the frequency and intensity of climatic extremes and is leading to intensified sea level variability (Cai et al., 2012; Moon et al., 2015). In particular, extreme low sea level events are predicted to double in occurrence (Widlansky et al., 2015). Low sea levels are associated with high atmospheric pressure, and thus are concurrently associated with low humidity and rainfall, which may increase the likelihood of mangrove mortality in mid-latitude ENSO influenced regions.

Low sea levels which result in hypersaline soil water in combination with low humidity and drought is a severe threat to mangroves due to their synergistic adverse effects on physiological functioning (Lovelock et al., 2017). These environmental conditions are implicated in the recent mortality events in Northern and Western Australia, which account for ~20% of globally reported mortality (Duke et al., 2017a, Harris et al., 2017, Lovelock et al., 2017, Lucas et al., 2018). These observed mortality events are consistent with the prediction that mangroves in the Caribbean, Central America, West and South Africa, the Persian Gulf, the Red Sea and Australia are particularly susceptible to mortality from increasing aridity under future climate change scenarios (Alongi, 2015; Jennerjahn et al., 2017).

3.3. Sea level rise, wave energy and sediment availability

Sea level rise is predicted to result in mangrove mortality in areas with low sediment accretion (Gilman et al., 2008), or where there are barriers to mangrove transgression landward (i.e. the coastal squeeze effect, Torio and Chmura, 2013). Yet there are few reports of sea level rise-driven mortality which are not associated with land-use change or other direct human influence. Sediment supply is critical to enable vertically accretion, thereby allowing mangroves to keep pace with sea-level rise (Kirwan and Megonigal, 2013, Krauss et al., 2014, Lovelock et al., 2015, Woodroffe et al., 2016). and thus reductions in sediment supply may lead to mangrove mortality. Sediment delivery to the coast is strongly influenced by river flows. Therefore, damming of rivers and other anthropogenic activities decreasing sediment supply to coastal ecosystems (Milliman and Farnsworth, 2013; Wong et al., 2014), as well as climate change associated reductions in river flows, could contribute to future mortality as resilience of mangroves is reduced.

Mangroves are also highly sensitive to wave energy (Barnard et al., 2015; Walcker et al., 2015; Albert et al., 2016). Waves can drive mortality due to erosion (Thampanya et al., 2006). Increasing wave heights associated with climate change have already been attributed to severe shoreline recession in the Solomon Islands (Albert et al., 2016) and large scale loss of mangrove forest area due to erosion have been observed with periods of increased wave energy during positive cycles of the North Atlantic Oscillation winter index (Walcker et al., 2015). Waves also reduce recruitment through dislodgement of seedlings (Balke et al., 2013), which can limit recovery after mortality events. Oceanic wind speeds have increased due to climate change (Wong et al., 2014), which affects wave heights, current regimes and upwelling systems (Narayan et al., 2010; Albert et al., 2016), all factors that could contribute to future mangrove mortality.

3.4. Multiple stressors

Several recent examples highlight mangrove loss associated with cumulative impacts from multiple stressors that cannot be separated. The largest reported area of mangrove tree mortality from herbivory occurred in the Mexico in 2010 (Sánchez et al., 2018). The mortality occurred in an area highlighted as at risk from cumulative impacts of stressors such as erosion and salt water intrusion (Sánchez et al., 2018). The gradual decline of mangroves to cumulative impacts of herbivores, pathogens and climatic extremes highlighted in a recent study in the Bahamas (Rossi, 2018), provides an example of how multiple minor stressors can cumulatively result in mortality to mangrove forests. Similar large scale dieback associated with combined climatic stressors and herbivory have also been reported in salt marsh (Silliman et al., 2005; He et al., 2017). In another recent example, Servino et al. (2018)

report a large scale mangrove mortality from a hailstorm occurring in forests stressed by El Niño associated drought over multiple years. As such, it is important to consider the synergistic effect of multiple stressors when assessing the vulnerability of mangrove forests to climate change.

Climate change has the potential to influence mangrove mortality through the complex synergistic changes in environmental parameters. In terrestrial forests, herbivory and disease may cause forest mortality in conjunction with the many cumulative stressors associated with climate change (Williams and Liebhold, 1995; Lindner et al., 2010, Young et al., 2017). Future mangrove mortality will be influenced by both direct and indirect interactions among global sea level rise, regional sea level variability, global change in temperature, evaporation and precipitation, increased cyclone latitudinal range, intensity and frequency and changes to wind energy, wave energy and sediment budgets. In addition there will be further complexity associated with interactions between natural and anthropogenic processes (Fig. 4, Alongi, 2015, Feller et al., 2015, Duke et al., 2017a; Lovelock et al., 2017).

4. Conclusions

Half of the historic 36,148 ha reported loss of mangrove forest from natural causes resulted from tropical cyclones. Increases in the frequency and intensity of storms may therefore be the greatest natural threat to mangroves in the future, particularly where this interacts in synergy with high rates of relative sea level rise (Lovelock et al., 2015; Albert et al., 2016; Ward et al., 2016), which can be exacerbated by reduced sediment supply and subsidence (Lovelock et al., 2015). Landward migration and poleward expansion, where possible, may reduce impacts on the extent of mangrove cover (Traill et al., 2011; Rogers et al., 2012; Osland et al., 2017b).

Since 2015, widespread areas of forest mortality have been linked to climatic extremes such as drought and sea level variability, which are now accounting for a rapidly increasing proportion of global forest loss. This review highlights the emerging importance of increasing extreme climatic events and variation in frequency and intensity of El Nino events in driving mangrove mortality (Duke et al., 2017a; Lovelock et al., 2017, Otero et al., 2017). Therefore, increasing synergistic impacts of intense storms and climate extremes may reduce resilience of mangroves and the ecosystem services they provide, particularly in subtropical latitudes.

It is important to note that the complex and interrelated changes to climatic variables may not lead to predictable environmental responses. For example, increased precipitation in low latitudes may be beneficial to mangroves, yet abrupt increases in sediment supply associated with rainfall and catchment land use change may be detrimental to mangrove forests. Extreme rainfall events in combination with changing land use practises may lead to increases in mangrove mortality due to smothering, yet may also increase mangrove resilience to sea level rise. We therefore highlight that synergistic impacts of anthropogenic activity and climate change may lead to unpredictable outcomes. Enhanced understanding of spatial variation in impacts and recovery using emerging remote sensing techniques (Lucas et al., 2017) will assist in managing coastlines exposed to increasing frequency of storms and climatic extremes.

Acknowledgements

This review was initiated with funding from the ARC (DP180101285, DP150103286). James Z. Sippo acknowledges support for this work through an AINSE Postgraduate Research Award. DTM acknowledges funding from the Australian Research Council which partially funds his salary (DE1500100581).

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